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NON-OVERLAPPING DISTRIBUTIONS OF SPIONID POLYCHAETES: THE RELATIVE IMPORTANCE OF HABITAT AND COMPETITION¹

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Abstract: The spionid polychaetes, *Pygospio elegans* Claparède, *Pseudopolydora kemp*i (Southern), and *Rhynchospio arenicola* Hartman are found in False Bay, Washington. Two species, *Pygospio elegans* and *Pseudopolydora kemp*i, co-occur in the high intertidal zone. The third species *Rhynchospio arenicola* occurs only in low intertidal areas. Reciprocal transplant experiments were used to test the importance of intraspecific density, interspecific density, and habitat on the survivorship of experimental animals. For all three species, only habitat had a significant effect. Individuals of each species survived better in experimental containers in their native habitat, regardless of the heterospecific and conspecific densities used in the experiments. The physical stresses associated with the prolonged exposure of the high intertidal site are experimentally shown to result in *Rhynchospio* mortality. From these experiments, habitat type is the only significant factor tested which can explain the observed distributions; the presence of confamilials has no detected effect on the survivorship of any species, suggesting that competition does not serve to maintain the patterns of distribution.

INTRODUCTION

With the rigorous use of experimental methods, soft-sediment researchers have begun to understand the determinants of the distribution and abundance of infaunal organisms. Numerous authors have critically demonstrated competitive interactions in such communities (Rhoads & Young, 1970; Woodin, 1974; Ronan, 1975; Myers, 1977; Peterson 1977, 1982; Peterson & Andre, 1980; Brenchley, 1981, 1982; Wilson 1981, 1983; Levin 1981, 1982). These studies largely deal with distributions on scales of mm to m. The data from these studies cannot be used to interpret larger scale patterns of abundance in embayments and along transects (Hobson, 1967; Johnson, 1970; Day *et al.*, 1971; Dauer & Simon, 1976; Brown, 1982). Few experimental data have been obtained which provide insight into the maintenance of these broad scale patterns.

Stemming from Darwin (1859), the notion that the strongest interspecific competition should occur among closely related species became nearly axiomatic in ecology. Interspecific competition was invoked indiscriminately to explain non-overlapping distributions of closely related species (e.g. McArthur, 1958; Schoener, 1974; Diamond, 1978). Experimental work has shown that such non-overlapping distributions are often properly attributed to interspecific competition (Hairston, 1951, 1980; Connell, 1961; Pianka, 1975; Dunham, 1980; Abramsky & Sellah, 1982; Schoener, 1982). However,

¹ Contribution No. 351 of Harbor Branch Foundation.

most ecologists do not rigorously subscribe to the primacy of interspecific competition in structuring communities (e.g. Smith & Balda, 1979; Woodin & Jackson, 1979; Schoener, 1982).

In this contribution, I describe a marine sand flat where two confamilial polychaetes exhibit non-overlapping distributions with that of a third confamilial species. Experiments were designed to assess the importance of interspecific competition and habitat in maintaining the observed distributional patterns.

STUDY SITE AND ORGANISMS

False Bay is an intertidal embayment on San Juan Island, Washington, U.S.A. The sediment in False Bay ranges from a fine sand in the upper intertidal to a well-sorted coarse sand at the mouth. Brenchley (1981) provides a map and detailed sediment data.

In the upper intertidal region (0.8–1.2 m above MLLW) two spionid polychaetes, *Pygospio elegans* Claparède (48 000/m²) and *Pseudopolydora kemp*i (Southern) (12 000/m²) are numerically dominant (Wilson, 1983). *Pygospio elegans* (hereafter *Pygospio*) is the smaller species, attaining lengths of 12 mm. *Pygospio* feeds by extending up to one-third of its body from its tube to gather detritus with its palps and mouth (Woodin, 1982; Wilson, 1983). *Pseudopolydora kemp*i (hereafter *Pseudopolydora*) attains lengths of 30 mm and feeds by extending its muscular palps from its tube to gather detritus on the sediment surface or in the water column (Taghon *et al.*, 1980; Woodin, 1982). Wilson (1983) has shown that each of these species experiences little competition with the other species because of lateral and vertical partitioning of space. Other macrofaunal organisms in the upper intertidal region include the polychaetes *Abarenicola pacifica* Healy & Wells and *Paraonella platybranchia* (Hartman), a multispecific group of oligochaetes, the amphipod *Corophium spinicorne* Stimpson and the cumacean *Cumella vulgaris* Hart.

In the lower intertidal zone, the spionid polychaete *Rhynchospio arenicola* Hartman (hereafter *Rhynchospio*) is a dominant organism (12 000/m²). *Rhynchospio* reaches lengths of 15 mm and feeds in a similar way to *Pygospio*, extending up to half of its body from its tube to gather sand grains and detritus with its mouth and palps (Woodin, 1982). Associated organisms include the tanaid crustacean *Leptochelia dubia* (Krøyer), the amphipod *Paraphoxus spinosus* Holmes, the bivalve *Transennella tantilla* (Gould), the holothurian *Leptosynapta clarki* Heding and the polychaete *Lumbrineris zonata* (Johnson).

The three spionids described above are rarely found together. Occasionally, *Rhynchospio* will be found in the high intertidal region with *Pygospio* and *Pseudopolydora* (< 10/m²). *Pygospio* is never found and *Pseudopolydora* is rarely found (< 10/m²) in the lower intertidal zone.

MATERIALS AND METHODS

To test the effect of conspecific density, heterospecific density, and habitat on the survivorship of each spionid, a reciprocal transplant experiment was performed. Experimental containers were constructed from plastic screening (1 mm mesh) and Hot Glue. The containers were cylinders 100 mm tall and 36 mm diameter (10 cm² in area). A bottom of plastic mesh was glued to each cylinder. The containers were filled with azoic sediment (prepared by freshwater immersion for 4 days). Spionids placed on the surface of the containers promptly burrowed and formed tubes. The containers were filled with prescribed numbers of animals and "planted" level to the sediment surface in the field. The containers did not interfere with ripple marks on the sediment surface and were not scoured by water currents. At termination, the containers were reclaimed and the enclosed organisms enumerated after sieving.

Normal (1 ×) experimental densities were based on normal field densities: 12 000/m² for *Pseudopolydora* and *Rhynchospio*, 48 000/m² for *Pygospio*. In this experiment, I treated *Pygospio* and *Pseudopolydora* together as an experimental unit since these species co-exist and experience negligible interspecific competition in the field (Wilson, 1983).

The survivorship of experimental spionids was tested as a function of three factors: intraspecific density, interspecific density, and habitat. For each spionid, four density treatments were established. *Rhynchospio* was established at one-half normal (1/2 ×) and normal (1 ×) densities in the absence of the upper intertidal spionids (0 ×) and in the presence of the comparable density of *Pygospio/Pseudopolydora* (1/2 × or 1 ×), thus yielding four different *Rhynchospio* treatments. *Pygospio* and *Pseudopolydora* were established together either at 1/2 × or 1 × both in the absence of *Rhynchospio* (0 ×) or in the presence of *Rhynchospio* at comparable densities (1/2 × or 1 ×). The treatment with all species present at normal density required the addition of 48 *Pygospio*, 12 *Pseudopolydora*, and 12 *Rhynchospio*. The four treatments for each species allow the testing of the effects of both conspecific density and heterospecific density. To test the effect of habitat, I performed the experiments above at both a high and low intertidal site. The sediment used in the treatments corresponded to the sediment at each experimental site.

Five replicates of each treatment were placed in the field on 21 July 1982 and reclaimed on 29 July. At termination, each container was sieved separately in the laboratory on a 500-μm screen and all organisms counted. For each species, survivorship data (number recovered/number introduced) were arc sin \sqrt{x} transformed and analyzed with a three-way analysis of variance (ANOVA) to test for significant experimental effects. Factor level means were compared by Sheffe post hoc comparisons (Zar, 1974).

To test the effect of intertidal exposure on *Rhynchospio* survivorship, *Rhynchospio* were established at 1/2 × densities in plastic beakers, 58 mm in diameter, and placed in running sea water at the Friday Harbor Laboratories. Azoic sediment from the low intertidal was used in the beakers. Each beaker received 32 *Rhynchospio*. Replicates from the experimental treatment were taken to the high intertidal region of False Bay

in the early morning (0400–0730) for 6 consecutive days (16 August until 21 August, 1982) just as the experimental area was exposed. (Tides in Puget Sound are classified as unequal semidiurnal tides and therefore the experimental site was exposed only once a day.) The beakers were placed in the sediment and were recovered in mid-afternoon shortly before the flooding tide covered them. The containers were brought back to the laboratory each day and placed in running sea water until the following morning. This procedure insured that no migration out of the beakers could occur in the field since *Rhynchospio* will not crawl out of their tubes when exposed at low tide. Also, the surface of the sediment in the beakers was 5 mm below the lip, precluding the possibility of emigration. Two control treatments were used. A transportation control tested for significant mortality associated with moving the beakers between the lab and the field. Each morning, replicates of the transportation control were taken to the field with the experimental replicates and then brought back to the laboratory to the sea table. A second control consisted of worms placed in beakers that were continuously maintained in running sea water. At the conclusion of this experiment, the three replicates of each treatment were sieved separately and surviving worms counted. Differences in the *Rhynchospio* survivorship for each treatment were tested for significance with a one-way ANOVA on $\arcsin \sqrt{x}$ transformed data, followed by Scheffe post hoc multiple comparisons.

RESULTS

The survivorship data from the reciprocal transplant experiment are given in Table I. For *Rhynchospio* (Table IA), the three-way ANOVA indicates that the effect of intra-specific density is not significant ($F_{1,37} = 0.09$, $P > 0.75$) nor is the effect of interspecific density ($F_{1,37} = 0.00$, $P > 0.95$). The effect of habitat (tidal level) is significant

TABLE I

Survivorships of experimental populations of the three spionid species in the reciprocal transplant experiment: $1/2 \times$ refers to half normal density, $1 \times$ to normal density; R denotes the presence of *Rhynchospio* and P denotes the presence of *Pygospio* and *Pseudopolydora*; means sharing the same letter are not different in Scheffe post hoc comparisons ($P > 0.05$).

		A. <i>Rhynchospio</i> survivorship			
		$1/2 \times$ R	$1/2 \times$ R-P	$1 \times$ R	$1 \times$ R-P
Habitat:	Upper	0.0 a	0.0 a	0.0 a	0.02 a
	Lower	0.33 b	0.33 b	0.32 b	0.23 b
		B. <i>Pygospio</i> survivorship			
		$1/2 \times$ P	$1/2 \times$ R-P	$1 \times$ P	$1 \times$ R-P
Habitat:	Upper	0.96 a	0.98 a	0.71 a	0.79 a
	Lower	0.24 b	0.39 b	0.19 b	0.17 b
		C. <i>Pseudopolydora</i> survivorship			
		$1/2 \times$ P	$1/2 \times$ R-P	$1 \times$ P	$1 \times$ R-P
Habitat:	Upper	0.72 a	0.63 a	0.71 a	0.82 a
	Lower	0.12 b	0.20 b	0.36 b	0.23 b

($F_{1,37} = 45.52$, $P < 0.001$). None of the four interactive effects is significant ($P > 0.05$ in all cases). In the upper intertidal experiment, only two *Rhynchospio* were recovered. It is not possible to know from these data if the poor recovery of *Rhynchospio* resulted from migration out of the experimental containers or from mortality of experimental organisms.

One can reject the hypothesis that *Rhynchospio* emigrated or died as a function of other organisms which immigrated into the containers. The most abundant immigrants were oligochaetes ($\bar{x} = 1.72/\text{core}$) and the cumacean *Cumella vulgaris* ($\bar{x} = 1.49/\text{core}$), both deposit-feeders. It is extremely unlikely that such low densities of animals would impel *Rhynchospio* to emigrate or die. The low survivorships of *Rhynchospio* in their normal lower intertidal habitat (Table IA) implies that net migration out of the containers was the primary process producing the low survivorships in the containers; one would expect high survivorship of *Rhynchospio* in their native sediments.

The survivorship data for *Pygospio* are given in Table IB. The three-way ANOVA reveals that the effect of conspecific density is not significant ($F_{1,38} = 0.94$, $P > 0.30$) nor is the effect of *Rhynchospio* density ($F_{1,38} = 0.13$, $P > 0.70$). The effect of habitat (intertidal site) is significant ($F_{1,38} = 41.98$, $P < 0.001$). None of the interactions of the main effects is significant ($P > 0.05$ in all cases).

The survivorship data for *Pseudopolydora* are presented in Table IC. From the three-way ANOVA, the effect of conspecific density ($F_{1,38} = 0.42$, $P > 0.50$), the effect of *Rhynchospio* density ($F_{1,38} = 2.23$, $P > 0.10$) and all interactive effects ($P > 0.05$ for all cases) are not significant. The effect of experimental site is highly significant ($F_{1,38} = 13.27$, $P < 0.001$). As expected (Wilson, 1983), *Pygospio* and *Pseudopolydora* both maintain high survivorships in all of the high intertidal treatments. In the low intertidal treatments, survivorships are reduced. I tested the hypothesis that non-spionid immigrants in the containers forced *Pygospio* and *Pseudopolydora* to emigrate. The only species that immigrated into the containers in significant numbers was the tanaid *Leptochelia dubia* ($\bar{x} = 7.72/\text{container}$). If *Leptochelia* were forcing *Pseudopolydora* and *Pygospio* to emigrate, one would predict a negative correlation of spionid abundances with *Leptochelia* abundances. There is no significant correlation between *Leptochelia* and *Pygospio* abundances (Pearson's $r = -0.068$, $P > 0.05$, $n = 19$) nor between *Leptochelia* and *Pseudopolydora* abundances ($r = 0.279$, $P > 0.05$, $n = 19$). The correlation between *Leptochelia* and *Rhynchospio* abundances is not significant ($r = 0.309$, $P > 0.05$, $n = 20$). Thus, this correlational analysis suggests that *Leptochelia* has no effect on the emigration of any of the experimental spionid polychaetes. A summary of all the experimental effects in the transplant experiment is given in Table II.

As a test of the hypothesis that the low survivorship of *Rhynchospio* in the high intertidal treatments (Table IA) could be explained by desiccation stress, I tested the ability of *Rhynchospio* in native sediment to survive the 8–10 h of exposure to air which is characteristic of the high intertidal site. Experimental data are presented in Table III. There is no significant difference between the two controls, indicating that the effects of transporting the worms to and from the field were insignificant. The experimental

effect is quite strong. Only one of 96 animals survived. These data provide strong evidence showing that the lengthy intertidal exposure in the high intertidal zone is inimical to *Rhynchospio* survivorship.

The low survivorship of *Pygospio* and *Pseudopolydora* is best explained by emigration from the experimental containers. In the laboratory, *Pygospio* and *Pseudopolydora* were maintained at ambient densities in low intertidal sediment. After 59 days, *Pygospio* had a mean survivorship of 0.83 and *Pseudopolydora* had a mean survivorship of 0.90. In this experiment, emigration from the containers could not occur. Thus, both species are capable of maintaining themselves in low intertidal sediment. The more parsimonious explanation for their low survivorship in the low intertidal containers is emigration rather than mortality.

DISCUSSION

The experiments described provide insight into the distribution of three closely related organisms. The results of the reciprocal transplant experiments (Tables I, II) accord with the pattern of distribution seen in the field. *Rhynchospio*, a low intertidal species, survived better in experimental containers in the lower intertidal site. Its poor survival in the high intertidal can be explained by the rigors and physical stresses associated with the prolonged exposure in such sites (Table III). *Rhynchospio* in the lower intertidal site did not exhibit high survivorship values, although they were significantly higher than survivorships in the high intertidal treatments. The low survivorship in the lower intertidal site is best explained by appeal to emigration out of the containers. None-

TABLE II

Summary of effects on survivorships of the three species in the transplant experiment: NS, *F* value non-significant ($P > 0.05$); **, *F* value significant ($P < 0.01$).

Effects	Species		
	<i>Rhynchospio</i>	<i>Pygospio</i>	<i>Pseudopolydora</i>
Intraspecific	NS	NS	NS
Interspecific	NS	NS	NS
Habitat	**	**	**
Interaction	NS	NS	NS

TABLE III

Survivorships of *Rhynchospio* in the physiological tolerance experiment: CONT, laboratory control; TC, transportation control; EXP, experimental field exposure treatment; means sharing the same letter are not significantly different in Scheffe post hoc comparisons ($P > 0.05$).

CONT		TC		EXP	
0.88	a	0.72	a	0.01	b

theless, a significant habitat effect is seen on *Rhynchospio* survivorship despite its relatively low survivorship in all of the experimental containers. *Pygospio* and *Pseudopolydora* survived better in high intertidal treatments than in low intertidal ones (Table I). The ability of both species to survive in low intertidal sediment in the laboratory suggests that emigration is the likely mechanism for their low survivorship within containers in the field.

Habitat, therefore, appears to be the most important factor of those tested in determining survivorship or persistence of the three confamilials. Importantly, Brenchley (1978) experimentally showed predation to be low in these communities. Among infaunal organisms, adults are often mobile and their movements have been shown to function in habitat selection (Holme, 1950; Levinton, 1977, 1979; Levin, 1981; Wilson, 1983). Wilson (1983) argues that habitat selection in such organisms occurs by a trial-and-error process in which the organisms can assess only their present habitat, not the habitat into which they might migrate. Such directed movement may be of considerable importance in interpreting the low survivorships of spionids in foreign environments (Table I). However, such movement in the field serves only to select habitats on small scales (< 1 m). The organisms are constrained by limited dispersal abilities. *Pygospio* reproduces asexually in False Bay (Rasmussen, 1953; Wilson, 1983) and dispersal is limited to distances of cm. *Pseudopolydora* females brood embryos to late stages (15–17 setigers) and dispersal is on a small scale (Blake & Woodwick, 1975; Myohara, 1979). For these two species, dispersal to the lower intertidal region is probably infrequent. However, once established, either of these two species potentially could rapidly build up a local population. The fact that such populations do not occur in the lower intertidal zone of False Bay attests to the inadequacy of that area as habitat for *Pygospio* and *Pseudopolydora*. The reproduction of *Rhynchospio* is poorly known for False Bay but based on studies from other areas (Carrasco, 1976; Levin pers. comm.), *Rhynchospio* has larvae which are planktonic for 1–2 wk. The larval stage is therefore more important in habitat selection for this species than the adult stage, but nothing is known about larval settlement cues in this species.

Contrary to what would have been predicted on the basis of competition theory, the presence of confamilial animals has no effect on the survivorship of any of the three species (Table I). At the experimental densities used, there were never any intraspecific or interspecific density effects. Thus, the non-overlapping distribution of *Rhynchospio* is not explicable by a process of competitive exclusion from the high intertidal by *Pygospio* and *Pseudopolydora*. Conversely, *Rhynchospio* (or low densities of the tanaid *Leptochelia dubia*) cannot exclude *Pygospio* and *Pseudopolydora* from the low intertidal region.

The invocation of competition in explaining patterns of infaunal distribution (e.g. Whitlatch, 1980) without experimental manipulation is open to doubt. If the present case is any guide, habitat characteristics may be more important than resident species in determining the distribution of infaunal organisms.

ACKNOWLEDGEMENTS

I wish to thank B. Brown, L. A. Levin, P. Linley, R. W. Virnstein, and S. A. Woodin for critically reading earlier drafts of this manuscript. A. O. D. Willows made the facilities of the Friday Harbor Laboratories available to me. This work was supported by a grant from the Theodore Roosevelt Fund of the American Museum of Natural History.

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